

MAMMALIAN SPECIES No. 616, pp. 1–8, 4 figs.

Orcaella brevirostris. By Pam J. Stacey and Peter W. Arnold

Published 5 May 1999 by the American Society of Mammalogists

Orcaella Gray, 1866

Orca [Orcaella] Gray, 1866:285. Type species *Phocaena (Orca) brevirostris* Owen in Gray, 1866.

Orcaella Anderson, 1871:142, footnote. Unjustified emendation.

CONTENT AND CONTEXT. Order Cetacea, Suborder Odontoceti, Superfamily Delphinoidea, Family Delphinidae. The genus also has been placed in the following families: Delphinapteridae, with beluga *Delphinapterus leucas*, by Kasuya (1973); Monodontidae, with beluga and narwhal *Monodon monoceros*, by Barnes (1984), Gaskin (1982) and Pilleri et al. (1989); the monotypic Orcellidae or Orcaelidae by Nishiwaki (1963, 1972). Placement in the Delphinidae is supported by osteology, facial and cranial sinus morphology (Arnold and Heinsohn, 1996; de Muizon, 1988; Heyning, 1989) and molecular data (Arnason and Gullberg, 1996; Gretarsdottir and Arnason, 1992; LeDuc, 1997; Lint et al., 1990; Messenger and McGuire, 1998). Within Delphinidae, it has been placed in the variably defined subfamilies Orcinae (Fraser and Purves, 1960) and Globicephalinae (de Muizon, 1988), the monotypic Orcellinae (Perrin, 1989), or as the sister taxon to all other delphinid genera (Messenger and McGuire, 1998). Arnason and Gullberg (1996), using cytochrome b sequences, placed *Orcaella* closest to the killer whale *Orcinus*, but they included only a limited number of delphinid genera in their analysis. LeDuc (1997), using representatives from all delphinid genera, also found the closest relationship to be between *Orcaella* and *Orcinus*, but the relationship was relatively distant and had low support in bootstrap analysis. A revision of the Delphinidae sensu lato is necessary before the position of *Orcaella* within the family can be resolved.

Orcaella brevirostris (Owen in Gray, 1866)

Irrawaddy Dolphin

Phocaena (Orca) brevirostris Owen in Gray, 1866:285. Type locality "east coast of India, the harbour of Vizagapatam" (= Vishakhapatnam).

Orcaella fluminalis Anderson in Gray, 1871:80. Type locality "River Irrawady."

CONTENT AND CONTEXT. Hershkovitz (1966) provides the most complete synonymy. One species, *O. brevirostris*, recognized, with *O. fluminalis* as a junior synonym (Lloze, 1973; Pilleri and Gehr, 1974). The following subspecies have been proposed:

O. b. brevirostris (Owen in Gray, 1866). Nominotypical subspecies.
O. b. fluminalis Ellerman and Morrison-Scott, 1951. Based on *O. fluminalis* Anderson in Gray, 1871.

Only the nominotypical subspecies generally is accepted. Australian specimens have four nodular nasal bones and a reduced mesethmoid plate, in contrast to the type specimen and other southeast Asian specimens (Arnold and Heinsohn 1996); the consistency of these and other geographical variations has not been documented. Additional morphologic and genetic studies are required before the validity of infraspecific taxa can be assessed.

DIAGNOSIS. A small delphinid, to 2.75 m length, with a bulbous, highly mobile head, broad flippers, small dorsal fin (height, 2.9–4.4% of body length), and obscure two- to three-tone color pattern (Fig. 1).

The skull (Fig. 2) has a short rostrum (43–45% of condylobasal length), with a well-developed mesethmoid crest. Teeth have an expanded crown but are not compressed. The dental formula is variable; published values include 13–17 (upper jaw)/12–14 (mandible—Anderson, 1879), 16–20/15–19 (Arnold and Heinsohn,

1996) and 19/15 (Lloze, 1973). The vertex of the skull of physically mature specimens retains juvenile features, with continued extensive dorsal exposure of frontal bones, triangular interparietal bone, and dorsal extensions of parietal bones. The mastoid portion of the zygomatic arch of the squamosal has a triangular ventral pad, serving as the attachment point for the tympanoperiotic bones; in other delphinids and porpoises (family Phocoenidae) the attachment is within a cavity formed by the squamosal, exoccipital, and basioccipital bones. Arnold and Heinsohn (1996) include a photograph of the holotype skull in dorsal view, whereas Pilleri and Gehr (1974) illustrate a skull from Thailand. Other photographs of skulls (Arnold and Heinsohn, 1996; Johnson, 1964; Marsh et al., 1989) are from northern Australian specimens.

The tympanic bulla (Fig. 3) is wide (about 54–61% of standard length of bulla), with a hemispherical outer posterior prominence and deep interprominentia notch. The posterior process of the tympanic bulla is directed posteriorly to posterolaterally. The cochlear

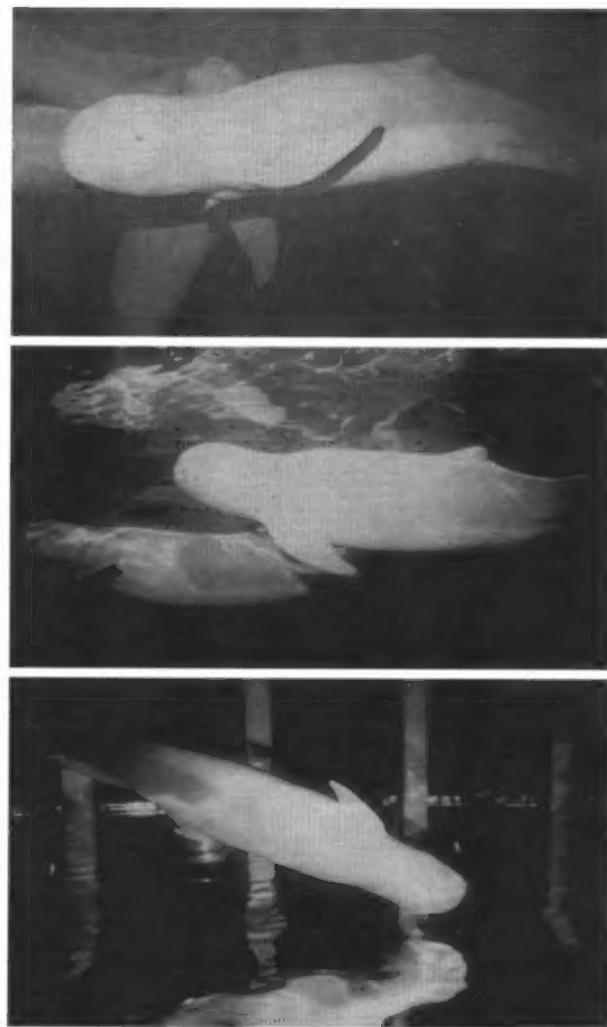


FIG. 1. Irrawaddy dolphins from the Mahakam River, Kalimantan, Indonesia, held at the Jaya Ancol Oceanarium, Djakarta. Photo by Anthony Preen.

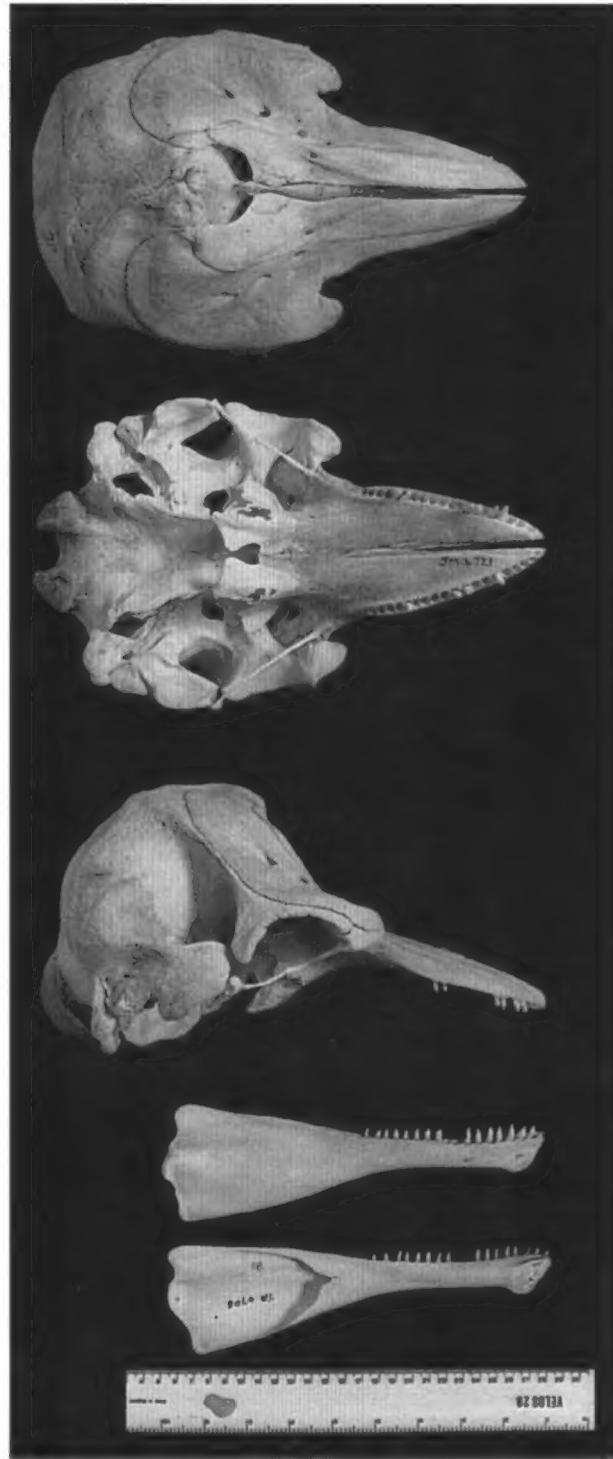


FIG. 2. Dorsal, ventral, and lateral views of cranium of Irrawaddy dolphin (QM JM4721; central Queensland coast, Australia; condylobasal length 312.8 mm) and lateral and medial views of left mandible (QM JM4708; central Queensland coast, Australia). Specimens held at Museum of Tropical Queensland. Photos by Bruce Cowell, from Arnold and Heinsohn (1996).

portion of the periotic is broader than long. The tractus spiralis foraminosus is prominent, and the aequeductus vestibuli is set at the base of an extensive funnel-shaped depression bounded by spongy bone (Arnold and Heinsohn, 1996; Kasuya, 1973).

GENERAL CHARACTERS. The adult Irrawaddy dolphin (Fig. 1) is about 2.1 m in length (Marsh et al., 1989). Maximum recorded length is 2.75 m for a male from Thailand (Bonhote,



FIG. 3. Ventral, lateral and medial views of left tympanoperiotic bones (QM JM4709; central Queensland coast, Australia). Standard length of bulla is 36.25 mm. Photos by Bruce Cowell, from Arnold and Heinsohn (1996).

1903). The largest male from northeast Australia was 2.70 m and the largest female 2.30 m ($n = 37$ —Arnold and Heinsohn, 1996).

Newborns have a mass of 10–12 kg. Adults 2.1–2.3 m long had a mass of 114–133 kg (Arnold and Heinsohn, 1996).

The head is smoothly rounded from blowhole to upper lip, without a beak. It is broadly triangular in dorsal view. The crescentic blowhole is displaced towards the left. The mouth runs postero-dorsad towards the eye. The neck crease is usually distinct, about half way between the eye and anterior insertion of flipper. Flippers are ca. 16% of body length, with a smoothly curved anterior margin and maximum breadth less than half of the length along the anterior margin of the flipper (Marsh et al., 1989). The dorsal fin, situated over halfway along the back, is small for a delphinid. Mean height ranged from 2.9% body length in Southeast Asian animals to 4.4% in northeast Australian animals (Arnold and Heinsohn, 1996). A midventral furrow extends from about the level of the flippers to the genital aperture. Breadth of the tail flukes is ca. 33% of the total body length. As is general in most cetaceans, the genital aperture is more anterior in males than females and there is a suggestion that males are larger than females, but no other sexual dimorphism has been demonstrated. Except for the

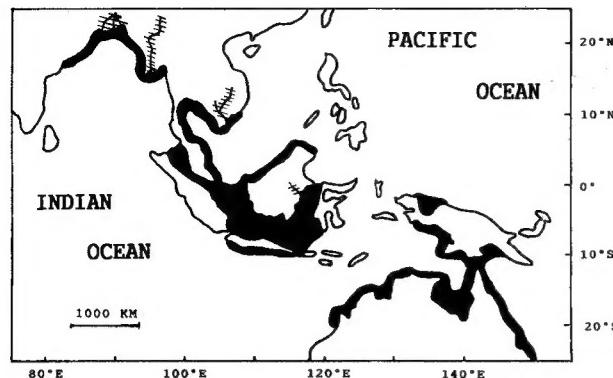


FIG. 4. Approximate geographic range of the Irrawaddy dolphin in coastal areas (dark) and major rivers (cross-hatched) based on the relatively few documented records.

height of the dorsal fin, there were no consistent differences in the external morphometrics of *Orcaella* specimens from northeastern Australia and southeast Asia (Arnold and Heinsohn, 1996).

Color pattern is obscure and may vary between populations. At one extreme, the color has been described as "dark slate-blue, nearly black" (Anderson, 1879:370), but this may be due to post-mortem darkening of the animals examined. Two males from Thailand were reported to be "between French grey and lead, slightly paler on the ventral surface" (Bonhote, 1903:43). Others have been described as "uniformly very dark grey" (Mörzer Bruyns, 1966: 370). However, animals from Kalimantan, Indonesia, appear to be lightly colored and subtly two-tone, with an extension of the abdominal field onto the flippers (Martin, 1990). Animals from northeast Australia have a subtle three-tone pattern, with a broad gray to blue-gray dorsal cape, white abdominal field between flippers and genital region, and intermediate light gray to brownish-gray field on the flanks (Arnold and Heinsohn, 1996). The head is very mobile, and can be strongly deflexed. The flippers also appear to be particularly mobile (Brownell et al., 1989).

DISTRIBUTION. *Orcaella brevirostris* occurs in the tropical-subtropical Indo-west Pacific, from the northwest Bay of Bengal to northeastern Australia (Fig. 4). It is a coastal species, also occurring in several major river systems of southeast Asia. Records are relatively few, although there are some areas of local abundance.

In India, the Irrawaddy dolphin has been recorded from Vizagapatam (= Vishakhapatnam) to the deltas of the Brahmaputra and Ganges Rivers (Anderson, 1879; James et al., 1989; Owen, 1866). The brackish Chilka Lake was an important habitat (Anandale, 1915), but Irrawaddy dolphins are now considered rare there (Dhandapani, 1992). The species has been recorded in relatively small numbers in coastal waters of Bangladesh (Haque, 1982; Kasuya and Haque, 1972), Myanmar (Smith et al., 1997b), peninsular Malaysia (Mörzer Bruyns, 1966; Stacey and Leatherwood, 1997), Singapore (Pilleri and Gühr, 1974), Thailand (Chantapornay et al., 1996; Stacey and Leatherwood, 1997), Cambodia (Lloze, 1973; Stacey and Leatherwood, 1997), Sarawak (Gibson-Hill, 1950; Pilleri and Gühr, 1974), Sabah (Dolar et al., 1997), Brunei (Gibson-Hill 1949, 1950; Pilleri and Gühr, 1974), and the Gulf of Papua (Dawbin, 1972). The population status is unknown in all these areas, but numbers appear to be declining in the Gulf of Thailand where they are concentrated in the Thale Sap (= Songkhla Lake) region (Perrin et al., 1996) and the Laem Sing area (Stacey and Leatherwood, 1997). Records from Sumatra, Java, Sulawesi, Kalimantan, and Irian Jaya are more numerous (Mörzer Bruyns, 1966; Stacey and Leatherwood, 1997); main concentrations in this area are said to be in coastal areas of Cilacap (Segara Anakan) on the southern coast of Java and in Kalimantan (Perrin et al., 1996). Records from northern Australia are numerous, extending from Broome, Western Australia to the east coast of Queensland as far south as the Brisbane River, Queensland (27°32'S—Freeland and Bayliss, 1989; Johnson, 1964; Marsh et al., 1989; Paterson et al., 1998).

The species has been recorded in the Irrawaddy (= Ayeyarwady) River, from near Prome to about 50 km above Bhamo, about

1,300 km upstream (Anderson, 1879; Leatherwood et al., 1984; Smith et al., 1997b; Thein, 1977). There are records of *O. brevirostris* from the Mekong River in Vietnam and Cambodia (including Tonle Sap) and a short distance into the Lao Peoples' Democratic Republic (Laos)—Baird et al., 1994; Baird and Mounshouphom, 1994; Lloze, 1973; Perrin et al., 1996; Smith et al., 1997a; Stacey and Leatherwood, 1997). Recent information suggests that numbers throughout the Mekong River, as well as in the Sekong River in Laos, have been declining. *O. brevirostris* has been recorded in the Mahakam River and Semayang Lake-Pela River of east Kalimantan, as well as the Kumay River of central Kalimantan (Tas'an and Leatherwood, 1984; Perrin et al., 1996). There is no fossil record.

FORM. There is no information on the epidermis. The skin of a specimen from the Irrawaddy River had scratch-like streaks "somewhat as in Risso's dolphin" (Anderson, 1879:358).

A near-term fetus had four to six brownish bristles on each side of the upper jaw about 12 mm above the lip; these were absent in an immature female, but their positions were indicated by pits (Anderson, 1879).

The musculature has not been described; Anderson (1879: plate 25a) indicated the relative proportions of epaxial and hypaxial muscles at the level of the pelvic bones.

The rostrum of the skull is unusually short for a delphinid. The braincase is relatively large, with os wurmiens (Lloze, 1982). The vertex of the skull retains juvenile features and is the most weakly telescoped of extant delphinoids (Arnold and Heinsohn, 1996).

The vertebral formula of six Australian specimens was 7 C, 12–13 T, 9–12 L, 28–30 Ca, total = 58–60, with 17–20 chevrons (Arnold and Heinsohn, 1996). The total vertebral count in southeast Asian animals was 62–63 (Anderson, 1879; de Smet, 1977; Lloze, 1973), but small sample sizes and discrepancies in defining the vertebral formula (Arnold and Heinsohn, 1996) limit comparisons. As in many delphinids, only the first two cervical vertebrae are fused; the transverse processes of C1 and C2 are much reduced, barely extending beyond the condylar facets in anterior view. Photographs of the complete vertebral column are given in Arnold and Heinsohn (1996).

There are 13–14 ribs, 1–2 of which may be free of the vertebral column; 7–8 are bicipital. There are 7 sternebral ribs, of which 4–6 articulate with the sternum (Anderson, 1879; Arnold and Heinsohn, 1996; Arvy and Pilleri, 1977). Pilleri and Gühr (1974) provide photographs of the ribs. The scapula is longer than deep; proportions of the acromion and coracoid processes appear to vary between Australian and southeast Asian animals (Anderson, 1879; Arnold and Heinsohn, 1996; Pilleri and Gühr, 1974). The sternum is highly variable, with a broadly concave anterior margin and anterior foramen; physically mature Australian animals may retain a compound sternum (Arnold and Heinsohn, 1996; Pilleri and Gühr, 1974).

The humerus is elongate, with an extensive deltopectoral tuberosity (de Muizon, 1988); the ulna usually has a distinct olecranon process (Arnold and Heinsohn, 1996). The phalangeal formula, based on several populations, is I 1–3, II 5–8, III 3–6, IV 3, V 0–2 (Anderson, 1879; Marsh et al., 1989).

Pelvic bones are situated between the 15th and 16th lumbar vertebrae; they act as attachment points for the crura of the penis, while the penis retractor originates on a strong fibrous band between the pelvic bones (Anderson, 1879).

There is a distinct preorbital lobe of the basicranial sinuses, with a dorsal extension intermediate in development between that in *Phocoena* and in the delphinid *Pseudorca* (Arnold and Heinsohn, 1996, based on dissection; Fraser and Purves, 1960). There is no anterior sinus, nor fusion of the preorbital and postorbital lobes to enclose the optic nerve (Arnold and Heinsohn, 1996), in contrast to enclosure of the optic nerve in the Delphininae sensu de Muizon (1988).

The bulbous head is predominantly connective tissue anteriorly, with limited development of the melon. The upper respiratory tract is delphinid in form (Arnold and Heinsohn, 1996), with apparent loss of the posterior nasal sac—a synapomorphy of the Delphinidae (Heyning, 1989).

There is no description of the brain. Anderson (1879), based on an interior cranial cast, indicated that the trigeminal, abducens, facial, and acoustic nerves were well developed, although he noted that the great thickness of these nerve trunks "is more apparent

than real" as the nerve cords "are accompanied by accessory vascular plexuses and thick sheaths" (Anderson, 1879:393). Photographs of sagittal sections of the brain are in Arnold and Heinsohn (1996).

Anderson (1879) illustrated a cast of the cochlear canal and semicircular canals. No other information is available on structure of sensory organs.

The larynx is tubelike and formed from extended arytenoid and epiglottidial cartilages as in other odontocetes (Green, 1972); the epiglottis is shorter than the arytenoid cartilages in the adult animal (Anderson, 1879). The trachea is short, with six generally incomplete cartilage rings between the larynx and bifurcation of the bronchi (Anderson, 1879). Bronchi and bronchioles have reinforcing cartilage rings (Anderson, 1879). A series of bronchiolar myoelastic sphincters are present (Lloze, 1973), as in other dolphins and porpoises (Slipper, 1962).

The heart of a 2.1-m adult was 12.7 cm wide across the base of the ventricles and 8.9 cm from the origin of the pulmonary artery to the apex of the left ventricle (Anderson, 1879). This relatively broad shape of the heart is found in other cetaceans and may be related to the general breadth and foreshortening of the ventral thorax in cetaceans (Slipper, 1962).

Right and left innominate (= brachiocephalic) arteries extend from the summit of the aorta, branching into subclavian and long, parallel carotid arteries (Anderson, 1879) as in other odontocetes such as *Globicephala* and *Phocoena* (Green, 1972). Anderson also noted a thoracic retial system along the vertebral column and in the intercostal spaces, as has been reported from other cetaceans, especially delphinoid odontocetes (Slipper, 1962).

The liver is divided into subequal right and left lobes but is otherwise smooth. Hepatic vessels, with thick fibrous walls and a supplementary vascular system, enter about the middle of the liver (Anderson, 1879). The pancreas, 10 cm by 3.8 cm in an adult animal, is placed obliquely between the right extremity of the first stomach chamber and the beginning of the duodenum. It opens into the common bile duct by two wide orifices. The common bile duct is lined with short columnar epithelium and mucus-secreting glands that are long, branching, and lobular (Anderson, 1879). The spleen of an adult animal was 5.8 cm by 2.5 cm, heart-shaped, with smaller lobes or splenules. It was attached to the lower border of the first stomach chamber (Anderson, 1879).

The stomach has three chambers, the last two with a narrow, funnel-shaped connecting channel (Anderson, 1879). These apparently correspond to the forestomach and fundic and pyloric chambers, but histology of the stomach chamber walls as described by Anderson (1879) is difficult to reconcile with more modern descriptions (Smith, 1972), possibly due to postmortem decomposition and inadequate fixation of Anderson's material. The duodenal sac is obvious. The kidneys are extensively lobulated, as in other cetaceans, with an average of 372 renules, usually clustered in groups of 3–4 (Lloze, 1973).

Anderson (1879) described six "os tineae," corresponding to the vaginal folds described generally in odontocetes (Harrison, 1969). The uterus is bicornuate, with a diffuse placenta. A full-term fetus was in the left horn, with the allantois occupying most of the right horn (Anderson, 1879), as in other odontocetes (Slipper, 1962). Anderson (1879:404–406) described the ovaries from fetal and mature specimens; however, his account is difficult to interpret and reconcile with more recent descriptions of cetacean ovaries. His histological material may have suffered from inadequate fixation and postmortem changes. There is no general description of the male reproductive tract.

The mammary gland of a pregnant female was ca. 24 cm long, 8 cm wide, and 6 mm thick, with a 5-cm-long, dilated sac above the nipple, into which the lactiferous ducts opened (Anderson, 1879).

The pulmonary glands have a fine network of connective tissue, forming the boundaries of spaces filled with lymphatic tissue. The glands are highly vascular and contain lymphatic sinuses (Anderson, 1879). There is no information on other endocrine organs, except for a brief description of gastric glands in Anderson (1879).

FUNCTION. The heart is 0.4–0.5% of the body weight (Lloze, 1973), comparable to values for delphinids such as common dolphin *Delphinus delphis* and bottlenose dolphin *Tursiops truncatus* (Sergeant, 1969). Rectal temperatures of a captive mother and calf were 36.5°C and 37.2°C, respectively (Tas'an et al., 1980).

Captive animals held at Jakarta, Indonesia were fed 5–8 kg of fish/day, an estimated 5–8% of their body weight (Tas'an et al., 1980).

Vocalizations of captive animals from the Mahakam River, Kalimantan consisted of a single-component sonar signal, with dominant frequency ca. 60 kHz. Pulse trains were regular, with repetition rates of 40 to 60 Hz. Captive animals did not approach fish thrown into the tank directly, but maneuvered around the fish, bending the head. This suggests that the sonar field may be quite narrow. No audible whistles or pure tones were recorded (Kamminga et al., 1983).

ONTOGENY AND REPRODUCTION. Courtship behavior has been reported from the Mekong River in Cambodia (11–12°N) from March to June (Lloze, 1973). The mating season in the Mahakam River population was considered to be April–June (Tas'an et al., 1980). Probable mating was observed in December along the upper reaches of the Ayeyarwady (Irrawaddy) River (Smith et al., 1997b).

Gestation period has been estimated at 14 months, based on two observations at the Jaya Ancol Oceanarium; however, no details as to how this was determined are given (Tas'an and Leatherwood, 1984). The pregnant female was aggressive towards other dolphins and aquarium staff during gestation.

A near-term fetus of 86 cm was recorded near Calcutta (ca. 22°N) in early June (Anderson, 1879). Laotian villagers claim that births occur in April and May (Baird and Mounoupoum, 1994); a 1.05 m long newborn was recorded in May at about 14°N (Stacey and Leatherwood, 1997). A near-term fetus of 91 cm was recorded near Townsville, Australia (19°S) in August (Marsh et al., 1989). Births at the Jaya Ancol Oceanarium, Jakarta (6°S) were in July, December (apparently stillborn), and February (Hendroku sumo, in Ellis, 1982; Tas'an et al., 1980). Thus, births may occur over an extended period at low latitudes, as documented for other odontocetes (Kasuya, 1995).

The birth of a captive *O. brevirostris* took 2 h 10 min from first appearance of the tail to first surfacing of the newborn for a breath (Tas'an et al., 1980). Stages of the birth were illustrated in Tas'an and Leatherwood (1984). Suckling was observed within 12 h of birth and occurred 45–75 times/day over the first 2 weeks. Fish were first taken at 6 months, with an intake of 1 kg/day at 7 months (Tas'an et al., 1980). The dolphin was fully weaned at 2 years of age (Marsh et al., 1989). In the first 7 months, the calf grew from 96 cm to 1.53 m length and from 12.3 to 45 kg in mass (Tas'an et al., 1980).

Age was determined for 18 dolphins from northeastern Australia (Marsh and Kasuya, in Marsh et al., 1989). Near adult size (2.1 m) was reached in 4–6 years; there is no information on age at sexual maturity. Among these 18 animals up to 28 dentinal layers were counted, suggesting that Irrawaddy dolphins "may live for at least 30 or so years" (Marsh et al., 1989:113).

ECOLOGY. Most records of feeding are inferred from field observations or, more commonly, from secondary reports of such observations. An Irrawaddy dolphin was observed in Chilka Lake, India, with its mouth open and cruising slowly back and forth in a shoal of the mysid shrimp *Macropsis* (= *Mesopodopsis*) *orientalis*, on which it was assumed to be feeding (Annandale, 1915; Kemp, 1915). Lao villagers assert that predators, assumed to be Irrawaddy dolphin, feed on the hind parts of freshwater catfishes (*Bagarius*, *Kryptopterus*, *Pangasius*), leaving the armored head to float at the surface (Baird and Mounoupoum, 1994). This was observed in 1994, when the freshly severed head of a cyprinid, *Cosmochilus harmandi*, was retrieved from the midst of Irrawaddy dolphins (Stacey, 1996). The Mahakam River population was said to feed on "carp" (a general term for cyprinids, not the true carp *Cyprinus carpio*, which was not recorded from the habitat by Tas'an et al., 1980).

There are only two studies based on examination of stomach contents. Two Irrawaddy dolphins from the Mekong River in Cambodia contained unidentified shrimps and five species of cyprinid fishes (*Puntius*, *Cirrhinus*, *Danigilas*, *Thynnichthys*—Lloze, 1973). Stomachs of ten dolphins from northeastern Australia contained schooling fishes found in the water column: Engraulidae (anchovies), Clupeidae (herrings), Chirocentridae (wolf-herrings), Hemirhamphidae (halfbeaks), Leiognathidae (ponyfishes), and Teraponidae (= Terapontidae, grunterns), as well as bottom-living, often solitary fishes: Apogonidae (cardinalfishes), Nemipteridae (threadfin

bream), Platyccephalidae (flatheads), Pomadasytidae (= Haemulidae, grunts), Psettodidae (Queensland halibut), Sillaginidae (smelt-whittings), and Synodontidae (lizardfish). All stomachs contained cephalopods (predominantly squid, cuttlefish, and octopus). Some stomachs contained unidentified shrimp (Marsh et al., 1989). Fish was considered the dominant prey item, but no quantitative data on feeding is available.

No ectoparasites have been recorded from *Orcaella* (Dailey and Brownell, 1972). Unidentified nematodes were reported from the stomachs of Australian animals (Marsh et al., 1989). Cobbold (1876) reported the fluke *Distoma lancea* Diesing from the duodenum of *O. brevirostris*. This species has been listed as *Amphimerus lancea* (Dailey and Brownell, 1972), but the synonymy is doubtful (Marsh et al., 1989). No pseudalidiid nematodes, which are widely reported from the respiratory tract and cranial sinuses of delphinoid odontocetes, have been recorded from *Orcaella* (Arnold and Heinsohn, 1996).

There is no information on diseases in the wild. Gastric ulcers, cirrhosis of the liver, "constitutional heart weakness," respiratory infection, fungal skin diseases, and "tonsilitis" were reported in captive animals (Tas'an et al., 1980:31).

Kammainga et al. (1983) suggested that *Orcaella* was forced inshore by more specialized dolphins, implying exclusion by interspecific competition. The basis for this statement was not given, and competitive exclusion is difficult to demonstrate without experiments. However, Stacey and Leatherwood (1997) did report that when captive humpback dolphins *Sousa chinensis* and Irrawaddy dolphins were held together, the former was dominant. Irrawaddy dolphins were frequently chased and confined to a small portion of the tank. Mörzer Bruyns (1966) observed that *Sotalia boreneensis* (? = *Sousa chinensis*) occurred in the same area as Irrawaddy dolphins, but that the schools never mixed. No observations of interactions between these genera in the field have been published. There are no confirmed predators on freshwater or marine populations of *Orcaella*.

Except for live-capture programs, captures of Irrawaddy dolphin appear minimal (Stacey and Leatherwood, 1997). Some were taken in India, where the oil was considered a remedy for rheumatism (Annandale, 1915). Legal protection occurs in India, Laos, Cambodia, Indonesia, and Australia; however, enforcement is a problem. There is, however, a generally positive attitude to dolphins in many southeast Asian countries, with beliefs that dolphins have saved drowning swimmers, offered protection against crocodiles, and assisted with fishing operations (Stacey and Leatherwood, 1997; Thein, 1977). Historically, fishermen along the Irrawaddy River claimed that particular dolphins were associated with individual fishing villages and chased fishes into their nets. Anderson (1879:361) was told by Colonel E. B. Sladen that "suits are not infrequently brought into the Native Courts to recover a share in the capture of fish, in which a plaintiff's dolphin has been held to have filled the nets of a rival fisherman." In this same river, Irrawaddy dolphins have been found to be involved in cooperative fishing with throw-net fishermen (Smith et al., 1997b).

Incidental catches in fishing nets have been reported from Bangladesh (Haque, 1982), Myanmar (Leatherwood et al., 1984; Smith et al., 1997b), Thailand (Andersen and Kinze, 1994), and the Lao-Cambodian border (Baird and Mounouphom, 1994), whereas it is suspected in Australia (International Whaling Commission, 1987). There has been a potentially significant incidental catch in shark control nets set in northeastern Australia (Paterson, 1990). There is not enough information from any locality to assess the impact of this incidental catch on populations of Irrawaddy dolphin, but it is of concern.

Habitat degradation includes increased use of nylon gillnets, increased vessel traffic (e.g., associated with logging in Kalimantan), reduction in food resources (e.g., by trawling in Gulf of Thailand), pollution, and sedimentation of coastal brackish lakes. Localized threats include use of explosives in fishing (Stacey and Leatherwood, 1997). Evidence for a decline in populations within Thailand, Laos and Cambodia, while largely anecdotal, is compelling (Perrin et al., 1996). In the Irrawaddy River, dolphin numbers currently appear to be stable, but potential threats, in the form of increasing use of gillnets and pollution from gold mining, are looming (Smith et al., 1997b).

Irrawaddy dolphins have been kept in captivity in Australia, Indonesia, Japan, and Thailand. Primary capture sources are coastal Thailand and Cambodia, as well as the Mahakam River-Semay-

ang Lake of Kalimantan. Tas'an et al. (1980) indicated that Irrawaddy dolphins were more subject to capture stress and changes in water conditions, as indicated by their refusal to feed, than the bottlenose dolphin *Tursiops*. Of 22 Irrawaddy dolphins captured in Kalimantan between 1974 and 1984, only two were alive in 1995 (Stacey and Leatherwood, 1997). Major problems with food and water quality have been recorded at Thai institutions, resulting in high mortality rates (Perrin et al., 1996). However, valuable life history data have been collected at the Jaya Ancol Oceanarium, and live births have occurred at several establishments (Perrin et al., 1996; Tas'an et al., 1980). This suggests that properly run captive programs could be self-maintaining.

BEHAVIOR. Surfacing behavior of Irrawaddy dolphins is usually unobtrusive (Dhandapani, 1992; Stacey, 1996). "The blow-hole is first seen, then at the end of inspiration the head disappears and the back comes into view, and is gradually exposed as far as the dorsal fin, but the tail flippers are rarely visible" (Anderson, 1879:360–361). However, many surface activities have been observed. In Laos, waving or slapping of flippers, tailwave or tail slap, breaches or partial leaps from the water, bubble blowing, sideways rolls, and spyhopping or pauses at the surface have been reported (Stacey, 1996; Stacey and Leatherwood, 1997). Frequent instances of water spitting also were observed. This intriguing behavior, the function of which is unknown, was first reported by Anderson (1879) and results in a well-defined column of water up to 1.5 m in height. Heyning and Mead (1996) suggested that blunt-headed odontocetes which employ suction feeding may hold water in the forestomach while they secure prey against the roof of the mouth, and then eject the water via the mouth. This could apply to *Orcaella*, which employs suction feeding, but "spitting" behavior has only been documented in freshwater populations of Irrawaddy dolphin.

Irrawaddy dolphins near Bhamo, Myanmar, stayed in the deep-water of the river, where the depth was 40–60 fathoms (73–110 m—Anderson, 1879). In a study in Laos where water depth was up to 35 m, the mean depth in which Irrawaddy dolphins were recorded was 18.5 m (Stacey and Leatherwood, 1997). In the western Gulf of Carpentaria, Australia, Irrawaddy dolphins were reported in depths of 2.5–18 m (Freeland and Bayliss, 1989). However, Irrawaddy dolphins have also been seen in very shallow water and were reported to frequently roll over and over on a shelf of sand at the margin of Chilka Lake, so that more than half of the body was out of water (Annandale, 1915). They also were reported to rush toward shore, with one individual observed to "strand itself on a flat shelf and remain for some seconds with its flippers and the forepart of its body practically out of water" (Annandale, 1915: 167).

Deep dive times range from 70–150 s (Anderson, 1879) to 12 min (Lloze, 1973). When 277 group dives were timed (time of disappearance of last dolphin in group to emergence of first dolphin in the group) in Laos, mean duration was 115.3 s (range, 19 s to 7.18 min); no differences related to group size were detected in duration of dives (Stacey, 1996). A swimming speed of 20–25 km/hour was reported when dolphins were being chased in a boat (Lloze, 1973).

Based on incidental observations, group sizes have been reported as 2–3 (Anderson, 1879), 5 (Bonhote, 1903), 3–4 (Annandale, 1915), 3–10 (Tas'an and Leatherwood, 1984), 3–6 (Mörzer Bruyns, 1966), <6 (Dawbin, 1972), and "up to 10–15" (Marsh et al., 1989:112). Groups ≤60 were reported by fishermen from the Irrawaddy River (Leatherwood et al., 1984). Three quantitative studies of group size are available. Mean school size in the western Gulf of Carpentaria, Australia, was found to be 1.9 ($n = 27$) in the dry season and 1.8 ($n = 43$) in the wet season (Freeland and Bayliss, 1989). In Laos a mean group size of 3.0 (range, 1–7; $n = 128$) during the dry season was found (Stacey and Leatherwood, 1997). A mean group size of 3.5 (range, 1–7; $n = 14$) was calculated from results of a study in the Irrawaddy River (Smith et al., 1997b).

There is little information on home ranges or territorial behavior. In the Irrawaddy River, reports from fishermen suggest that at least some dolphins maintain discrete home ranges (Smith et al., 1997b). One home range of about 35 km in length was reported to contain four dolphin groups and another of similar size, two groups. Frequent mixing between groups is reported.

There is little information on feeding behavior, due to the generally turbid habitat of the species. Observations of captive animals

indicate that food may be taken into the mouth by suction (Tas'an et al., 1980). This may be a general feature of blunt-headed odontocetes (Heyning and Mead, 1996). The teeth have been found to be ground to a flat surface (Anderson, 1879); however in the Mahakam River population teeth remain unerupted even in adult dolphins (Tas'an et al., 1980). River terns (*Sterna aurantia*) were regularly observed over Irrawaddy dolphins in Laos, sometimes swooping down to pick up scraps from the water surface (Stacey, 1996).

Irrawaddy dolphins were reported to frequently accompany river steamers, "careering in front and alongside of them, as is the custom of dolphins of the sea" (Anderson, 1879:360). This behavior has not been reported recently. A significant increase in dive times was documented when large motor vessels were within 100 m of Irrawaddy dolphins in Laos (Stacey and Leatherwood, 1997).

Diel migrations were recorded from Semayang Lake to the Mahakam River at 0500–0900 h and back to the lake at 1800–2000 h (Tas'an and Leatherwood, 1984). Dolphins' use of a study site in the Mekong River decreased from dawn to dusk daily (Stacey, 1996). Irrawaddy dolphins at the mouth of the Belawan Deli River, Sumatra were reported to swim inward against the ebb tide and outwards against the flood tide (Mörzer Bruyns, 1966).

Captive animals have been seen swimming slowly, with one eye closed (Tas'an et al., 1980); this is consistent with observations of sleeping in some other captive odontocetes (Connor and Micklenthwaite Peterson, 1994).

Seasonal migrations are poorly documented. In the Irrawaddy River, the time of highest water levels is from May to October, with a peak in August and September. At Pagan, dolphins were reported moving north in September–October and south in July–August. During high water levels, dolphins were reported to prefer the delta of the river (Leatherwood et al., 1984). In India, Irrawaddy dolphins reportedly left Chilka Lake during the latter part of the rainy season in August–October (Annandale, 1915). Sightings in a recent survey of Chilka Lake (Dhandapani, 1992) occurred only in winter and summer.

GENETICS. Studies using immunological and electrophoretic data concluded that *Orcaella* was a delphinid and distinct from both narwhal and beluga (Lint et al., 1990). *Orcaella* has a nucleotide base pair length of about 1580, found only in delphinids (Gretarsdóttir and Arnason, 1992). *Orcaella* was clearly placed in the Delphinidae when the complete cytochrome B gene sequences in 20 odontocetes and 8 mysticetes were compared (Arnason and Gullberg, 1996).

CONSERVATION STATUS. The species is listed as IUCN category K, for Insufficiently Known (Klinowska, 1991). The only attempt to rigorously assess population size, using aerial surveys, was in the western Gulf of Carpentaria, Australia (Freeland and Bayliss, 1989). The estimate was ca. 1,000 animals, but this figure has been questioned (Perrin et al., 1996) because of the difficulty in identifying species of tropical dolphins from the air, especially in very turbid water. Elsewhere, populations have been estimated as 25–30 dolphins near the Cambodian-Lao border (Perrin et al., 1996), 100 in Songkhla Lake, Thailand (Stacey and Leatherwood, 1997), 68 in the Mahakam River (a decline from the earlier estimates of Tas'an and Leatherwood, 1984), 30 in Segara Anakan, Indonesia (Perrin et al., 1996), and ca. 20 dolphins in Chilka Lake, India (Dhandapani, 1992). The reliability of some of these estimates is probably low, but available evidence suggests that Irrawaddy dolphins, while widespread, may be uncommon throughout much of their range, and that at least some of the populations in southeast Asia are in serious decline.

REMARKS. The name *Orcaella* is the diminutive of *Orca*, an apparent reference by Gray (1866) to similarities of the Irrawaddy dolphin skull to that of the killer whale, then known as *Orca*. The specific name, *brevirostris*, refers to the short rostrum of the skull.

Arnold and Heinsohn (1996) argued that the author citation for *O. brevirostris* is "(Owen in Gray, 1866)," based on application of article 50 and recommendation 51B of the International Code of Zoological Nomenclature (Ride et al., 1985). Circumstantial evidence suggests that the specific name *fluminensis* was first published in Gray (1871) rather than Anderson (1871), as indicated by Hershkovitz (1966). However, as Gray's publication relied entirely on

Anderson for the name and information, the author citation should be "Anderson in Gray, 1871."

In Indonesia, the Irrawaddy dolphin is known as *ikan pesut* or *pesut Mahakam*; it is the provincial symbol of East Kalimantan (Perrin et al., 1996). The Malaysian name is *lumba lumba* (Watson, 1981). In Laos, it is called *pa kha*, the Lao Loom word for dolphin. In Thailand, one of its names is *pla loma hooa baht*, because its rounded head is thought to resemble the shape of a monk's bowl, a *hooa baht* (Baird and Mounouphom, 1994).

Information on the Irrawaddy dolphin is sparse and depends on historical accounts such as Anderson (1879) and Annandale (1915), with only a few recent observational studies (Lloze, 1973; Stacey, 1996). Life history data is based on examination of a relatively few animals from northeastern Australia (Marsh et al., 1989) and limited observations on captive animals (Tas'an et al., 1980). Most observations need to be confirmed and extended.

We thank V. Harrison, at the Queensland Museum library, Brisbane, for locating literature references and J. G. Mead, Smithsonian Institution, for information on the publication date of Gray (1871). A. Preen, James Cook University of North Queensland, allowed us to use his photograph of live *Orcaella*. Photographs of the skull and tympanoperiotic bones are used with permission of the Queensland Museum. We also thank J. Heyning for his review of the manuscript.

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